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EXPERIMENTAL STUDIES ON THE DURATION OF LIFE

V. ON THE INFLUENCE OF CERTAIN ENVIRONMENTAL FACTORS ON DURATION OF LIFE IN *DROSOPHILA*¹

PROFESSOR RAYMOND PEARL AND SYLVIA L. PARKER

A. INFLUENCE OF VENTILATION ON DURATION OF LIFE

THE standard method of handling *Drosophila* cultures, as described by Pearl and Parker (27), includes the plugging of the mouth of the bottle with absorbent cotton to prevent the escape of the flies. The theory of this practice, which is the custom in Morgan's laboratory, presumably is that air will pass in and out through the plug while the flies can not. No physicist or ventilation engineer would, we believe, accept this theory. Many years ago the senior author had occasion to make some observations on the ventilation of curtain-front poultry houses, and soon came to the conclusion that curtains of one thickness only, of the very porous jute bagging which is used for bran sacks, are practically nearly as effective in *preventing* the natural unforced circulation of air as a half-inch pine board would be. We may be sure that the plug of cotton used in *Drosophila* bottles will be an even more certain preventative of the natural unforced circulation of air. Theoretically one may perhaps hold that there is *more* circulation of air with a cotton plug than there would be with a cork stopper, but the difference must be infinitesimal.

¹ Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, Johns Hopkins University, No. 67.

In the systematic survey which we are making, at the beginning of our experimental study of duration of life, it seemed desirable to test the influence upon this character of degree of natural ventilation of the bottles. It is the purpose of this first section of this paper to present the results of some experiments on this point.

Material and Methods

The experiments were carried out in two series. For the first, wild type flies of our Old Falmouth stock (Pearl and Parker (27)) belonging to Line 107, the duration of life constants of which have been given by Pearl and Parker (32), were used. These flies were of the 25th pedigreed generation. Eighteen mass matings of the flies of this line were started for the present experiments on March 13, 1922, and the flies to be used emerged March 23-30, 1922.

For the second series short-lived flies of Quintuple stock (Pearl and Parker (27)) were used, in the 27th pedigreed generation. Twenty-five mass matings of Quintuple line 405 were started April 10, 1922, and six mass matings of mixed Quintuple stock were started April 11, 1922. The flies for use in the experiment emerged April 22-27, 1922.

The procedure in making up the experiments was as follows: The flies were counted out each morning upon emergence into our standard one ounce screw top shell vials used in the determination of duration of life (Pearl and Parker (27)). Fifty flies were put in each bottle. The wild type flies were counted in through the counting tube described in these Studies, III (Pearl and Parker (44)). The Quintuple flies move through the tube so slowly, however, that there is time for moisture to condense and accumulate on the walls of the tube, killing some of the flies by drowning, and injuring others. Consequently the flies of this type were etherized and counted into the bottles. It has been shown in these Studies, III, that such etherization has no measurable

influence on duration of life. Each day's flies were divided equally between control and experimental groups. Fertility in the Quintuple flies is so low that even with the large number of matings the hatches on some days did not equal 100 flies. It thus resulted that there were a few bottles of the Quintuples with fewer than 50 flies to the bottle: 1 case with 40 flies in control and 40 in the experimental bottle, 1 with 37 flies in each bottle, and 1 with 23 flies in each bottle.

The *control* bottles were plugged with cotton in the ordinary way. The experimental, ventilated bottles were covered with one layer of silk bolting cloth of No. 48 mesh (48 meshes to the linear inch), this being the largest mesh which could be used without any possibility of a fly squeezing through the openings. The cloth was held firmly and evenly in place by an aluminum screw cap in the top of which a central hole a little more than $\frac{3}{4}$ inch in diameter had been punched out. This is practically the internal diameter of the shell vials which we use.

Both control and ventilated bottles were carried in 25° incubators, and all other procedure was that which has been described by the authors (27) as standard in the work of this laboratory on duration of life in *Drosophila*.

Results

The observed l_x distributions (survivors out of 1,000 starting together) for the wild type Old Falmouth Line 107 are given in Table I, together with the absolute numbers of flies on which the distributions are based.

These distributions of Table I are shown graphically in Fig. 1.

It is evident at once that the flies in the well-ventilated bottles outlive those in the ill-ventilated. Their expectation of life is greater at every age. The magnitude and significance of this difference can best be appreciated from the constants of duration of life set forth in Table II.

TABLE I

SURVIVORSHIP DISTRIBUTIONS (l_x) OF VENTILATED AND CONTROL FLIES
Old Falmouth, Line 107

Age in days	Number of survivors up to indicated age.	
	Ventilated	Control
1	1,000	1,000
7	986	984
13	970	969
19	946	929
25	900	846
31	804	730
37	697	615
43	589	485
49	480	397
55	371	292
61	278	195
67	185	119
73	103	44
79	12	2
85	0	0
Absolute number of flies	946	931

TABLE II

FREQUENCY CONSTANTS OF d_x DISTRIBUTIONS
Wild Type, Line 107

Group	Mean	Standard Deviation	Coefficient of Variation
Control.....	43.66 $\pm$.39	17.63 $\pm$.28	40.38 $\pm$.73
Ventilated.....	47.92 $\pm$.40	18.22 $\pm$.28	38.01 $\pm$.67
Difference.....	+ 4.26 $\pm$.56	+ .59 $\pm$.39	- 2.37 $\pm$.99

There is clearly a significant increase, amounting roughly to 10 per cent., in the mean duration of life, or expectation of life at emergence, in the flies in the ventilated as compared with the unventilated bottles, all other conditions both genetic and environmental having been the same in the two series.

That the increased amount of fresh air is the cause of the difference is evidenced by the behavior of the flies. In the ventilated bottles the flies tended at all times to congregate on the under side of the bolting cloth going down to the bottom for food occasionally, but otherwise exhibiting a strong preference for the region about the

mouth of the bottle, where the diffusion of air between inside and outside was going on most rapidly. This behavior is in no way characteristic, in our experience, of flies in the bottles stoppered with cotton. In those there

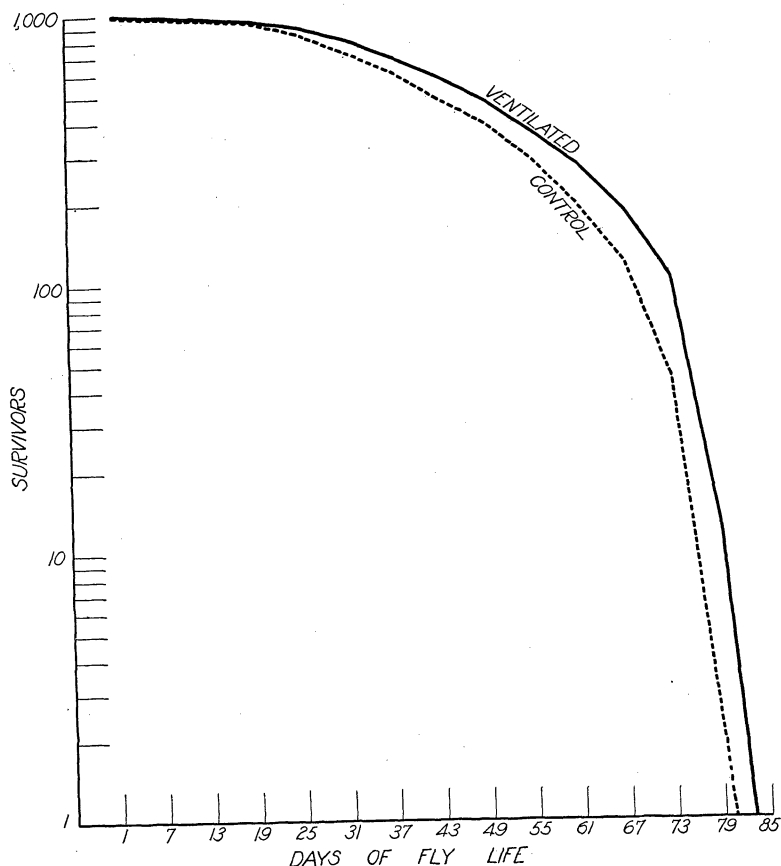


FIG. 1. Survivorship (l_x) lines for ventilated (solid line) and control (broken line) flies.

is generally a fairly even distribution of flies throughout the bottle, with such tendency towards concentration as there is, in the direction of the bottom near the food rather than the top.

In Table III are presented the survivorship distributions for the Quintuple flies. Because of their much shorter life span, as shown in the life tables of the first

one of the Studies (27), a shorter abscissal interval has been used in the grouping. The figures for Quintuple stock flies, and for an inbred Quintuple line (No. 405) are given separately.

TABLE III

SURVIVORSHIP DISTRIBUTIONS (l_x) OF VENTILATED AND CONTROL FLIES
Quintuple Stock and Line 405

Age in Days	Number of Survivors up to Indicated Age in			
	Stock Ventilated	Stock Control	Line 405 Ventilated	Line 405 Control
1.....	1,000	1,000	1,000	1,000
4.....	993	992	783	878
7.....	816	812	422	443
10.....	213	368	62	90
13.....	81	158	18	36
16.....	44	143	9	14
19.....	29	113	9	5
22.....	22	83	4	0
25.....	22	60	4	—
28.....	22	30	0	—
31.....	22	23	—	—
34.....	15	23	—	—
37.....	0	15	—	—
40.....	—	15	—	—
43.....	—	8	—	—
46.....	—	8	—	—
49.....	—	8	—	—
52.....	—	0	—	—
Absolute number of flies	136	133	209	221

The calculated constants from the d_x distributions are given in Table IV.

TABLE IV

FREQUENCY CONSTANTS OF d_x DISTRIBUTIONS
Quintuple Stock and Quintuple Line 405

Sort	Group	Mean	Standard Deviation	Coefficient of Variation
Quintuple stock..	Control.....	11.07 $\pm$.41	7.04 $\pm$.29	63.58 $\pm$ 3.54
	Ventilated.....	9.34 $\pm$.26	4.57 $\pm$.19	48.92 $\pm$ 2.43
Difference.....		— 1.73 $\pm$.49	— 2.47 $\pm$.35	— 14.66 $\pm$ 4.29
Quintuple (line 405).....	Control.....	6.90 $\pm$.13	2.90 $\pm$.09	42.09 $\pm$ 1.57
	Ventilated.....	6.78 $\pm$.14	2.99 $\pm$.10	44.06 $\pm$ 1.71
Difference.....		— .12 $\pm$.19	+ .09 $\pm$.13	+ 1.97 $\pm$ 2.32

The situation here is evidently quite different from what obtained with the wild type flies. The Quintuples lived somewhat longer in the control bottles than in the ventilated. In the case of flies from stock, the difference in the means amounts to 1.73 days, and is 3.5 times its probable error. The numbers are, however, small, and as an examination of Table III shows, the long survival of 2 individuals in the control series after age 34 accounts for a considerable part of the difference in the means. With a larger experimental sample much of the difference in the means would, we feel sure, disappear. The influence of these same two individual flies is clearly seen in the greatly increased variability of the control series over the ventilated in the stock groups.

In general we are of the opinion that in the case of Quintuple flies the difference in ventilation represented by a bolting cloth screen versus a cotton stopper has no significant influence upon duration of life. The results with extremely short-lived line 405, we regard as typical of what one should expect with Quintuple flies in this sort of an experiment.

The reason for the difference between wild type and Quintuple flies in their response to ventilation is founded, in our opinion, upon the normal differences in behavior between the two types. In Quintuples the wings do not function (the wing mutation in this stock is Vestigial). The consequence is that these flies are much less active, and generally appear to live on a lower metabolic plane, than wild type flies. Their oxygen needs are presumably smaller, and it would therefore be reasonable to expect that they would not show the difference in duration of life with increased ventilation that the wild type flies do. In this connection, it should be noted that their actual behavior in this experiment was in accordance with the view here suggested. They showed no such definite tendency to congregate at the top of the bottle under the bolting cloth as the wild type flies did. Their distribution was about the same in ventilated as in the control

bottles. Another consideration is that genetically Quintuple carries factors for very short life. These genes appear, in our experience with these flies, to be the overwhelmingly important factors in determining their length of life. No environmental factor, however favorable, makes much difference in their duration of life.

Summary

In experiments involving the determination of the duration of life in 2,576 individual flies, it has been found that in the case of *Drosophila* of wild type (*i.e.*, carrying no mutations so far as known), an increase of roughly 10 per cent. in the mean duration of life is brought about by increasing the ventilation of the culture bottles, by covering the mouth with one layer of No. 48 mesh bolting cloth, as compared with the use of cotton plug stoppers as is the usual practice in the culture of *Drosophila* in the laboratory. Owing, in our opinion, to fundamental differences in behavior, no such difference appears in the case of Quintuple flies.

B. CAN THE DURATION OF LIFE BE INCREASED BY EMBRYONIC JUICE?

If the theory of senescence and natural death which the senior author has developed in his "Biology of Death" (1-7) is true, one consequence of it should be that it might be possible to increase the duration of life, if by appropriate means one could restore the normal functional balance of the parts of the body after changes had set in with advancing age. Might it not be possible, by the use of X-rays for example, at the right stage of the life curve, and in proper dosage, to destroy cells, or perhaps even parts of tissues, which have got out of proper functional balance, and thus pave the way to their replacement by regeneration with fresh, "young" cells or tissues? In this way the life of the whole organism might be prolonged. The work of Frisch and Starlinger (45) with blood suggests that such a result might at least

be hoped for. In view of the known facts as to the potential immortality of tissue cells in cultures *in vitro*, and the apparent reason for the difference in the behavior of the same cells in respect of duration of life when they are in the multicellular body, all of which has been rather fully discussed by Pearl in the "Biology of Death" (*loc. cit.*), it would seem that this is a line of experimentation well worth following. We have a number of experiments along this line now in progress, particularly with X-rays, which we expect later to report upon. Some of the purely preliminary work has already been finished, and we wish in this paper to report one piece of it.

The brilliant researches of Carrel and his coworker Ebeling (*cf.* 46, 47) on the duration of life of cells in cultures *in vitro* have brought to light the extraordinarily interesting and presumably important fact that for the continued life of such cultures it is apparently essential to have in the culture medium a small amount of embryonic juice. In just what manner this functions is not yet clear, but the necessity of its presence seems well established.

It occurred to us in our preliminary work on prolongation of life in *Drosophila*, or as it is perhaps better to put it, on changing the form of the l_x line of the *Drosophila* life table, to see whether embryonic juice, applied at a point on the l_x curve after senescence had definitely set in, would have any effect upon the subsequent course of the curve, or in other words, upon the duration of life of the organism as a whole, comparable to its effect upon the life of cells in culture. The ideal way, of course, in such an experiment would be to get the embryonic juice to the tissues of the fly by a par-enteral route, but as no practical method of doing this occurred to us, we decided to feed it, and see if any results followed.

Material and Methods

The flies used in the experiment were all wild type, of Old Falmouth stock, and belonged to Line 107, pedigree

bred for 21 generations. The individuals for the experiment came from 20 mass matings of 3 pairs of parents each from this line. The bottles were started December 16, 1921, and the flies used in the experiment emerged December 28, 1921, to January 9, 1922.

The flies were counted through the counting tube into our standard shell-vials in groups of 50 each. Each day's bottles were divided into three groups at the beginning of the experiment, but all had the same regular treatment until the flies in them were 30 days old. This is a point where the *l_x* line is beginning distinctly to turn downward. . From that time on until the end of their life one series of flies was given chicken juice in their food, and one series the juice and pulp of crushed *Drosophila* larvæ. The chick embryos used were 14 days old. The juice was extracted in a beef-juice extractor, and added to the regular food at the rate of approximately 2 c.c. to 100 c.c. of food. With the *Drosophila* larvæ, the whole pulp was used, and that too was added to the regular food at the rate of approximately 2 c.c. to each 100 c.c. of food. All the flies, experimental and control, were transferred every day to fresh food, made up that day, except on Sundays.

On Feb. 8 an accident happened to the incubator at the source of our chicken supply,² so that for 12 days no chickens were obtainable.

In all particulars except those specified above, the procedure in these experiments was the standard technique of this laboratory in duration of life work described in (27).

Results

The survivorship distributions are given in Table V, on the basis, *A*, of 1,000 starting at emergence, and, *B*, of 1,000 starting at age 31 days, that is at the time when the experimental feeding began.

² We are greatly indebted to our colleagues, Dr. and Mrs. Warren H. Lewis, for furnishing us with chicken material for this work.

TABLE V
SURVIVORSHIP DISTRIBUTIONS (l_x) OF GROUPS OF DROSOPHILA FED
IN DIFFERENT WAYS

Old Falmouth Stock, Line 107

Age in Days	Number of Survivors up to Indicated Age in					
	Controls		Chicken Juice		Larval Pulp	
	A	B	A	B	A	B
1.....	1,000	—	1,000	—	1,000	—
7.....	975	—	970	—	970	—
13.....	945	—	935	—	930	—
19.....	884	—	873	—	858	—
25.....	797	—	784	—	719	—
31.....	616	1,000	648	1,000	591	1,000
37.....	491	796	456	703	464	785
43.....	362	588	313	484	283	479
49.....	286	465	246	380	210	356
55.....	212	345	198	306	156	264
61.....	156	253	152	234	116	196
67.....	120	197	110	170	82	140
73.....	59	96	58	89	46	78
79.....	21	34	24	38	28	48
85.....	7	11	9	14	3	5
91.....	1	2	0	0	1	2
97.....	1	2	—	—	0	0
103.....	0	0	—	—	—	—
Absolute number of flies.....	1,013	—	983	—	994	—

The biometric constants of duration of life calculated from the d_x distributions are given in Table VI.

TABLE VI
BIOMETRIC CONSTANTS FOR DURATION OF LIFE IN DROSOPHILA UNDER DIFFERENT CONDITIONS OF FOOD. A. FROM EMERGENCE.

B. FROM AGE 31 DAYS ON

Class	Group	Mean (in days)	Standard Deviation (in days)	Coefficient of Variation
A.....	Control.....	39.60±.40	18.76±.28	47.38± .85
	Chicken juice.....	38.66±.40	18.61±.28	48.12± .89
	Larval pulp.....	36.74±.39	18.01±.27	49.03± .90
B.....	Control.....	19.72±.40	14.66±.28	74.35±1.62
	Chicken juice.....	17.51±.40	15.05±.27	85.96±2.06
	Larval pulp.....	17.12±.39	14.03±.28	81.98±1.94

It is evident that there are no large differences in mean duration of life between any of the groups. The l_x distributions and the constants are closely similar throughout. This is true whether the whole life is taken, or the expectation after age 31. The exact nature of the differences is shown in Table VII.

TABLE VII
DIFFERENCES IN MEANS OF TABLE VI

Class	Difference Taken	Value of Difference	Diff./P.E. Diff.
A.....	Control—chicken juice.....	.94 ± .56	1.66
	Control—larval pulp.....	2.86 ± .55	5.15
	Chicken juice—larval pulp.....	1.92 ± .56	3.46
B.....	Control—chicken juice.....	2.21 ± .56	3.93
	Control—larval pulp.....	2.60 ± .56	4.67
	Chicken juice—larval pulp.....	.39 ± .56	.69

The control group had slightly the greatest duration of life, both as a whole, and from the time of the beginning of the special feeding on. The flies fed larval pulp had the worst expectation of life, with those fed chicken juice in an intermediate position. None of the differences, however, is large. That some of them are significant statistically probably means no more than that the changed food is not quite so favorable for the flies as the normal, standard food. The numbers involved are large relatively, and the probable errors consequently small.

We must then conclude that the administration of embryonic juice in the manner, amount and time in the life cycle, which defined its administration in these experiments, does not bring about any prolongation of the life of the whole organism, comparable to its effect in tissue cultures *in vitro*. This does not necessarily mean that under other conditions of administration or dosage an effect in this sense might not be produced. We believe, however, that it is not probable that any prolongation of life can be brought about by this method, for the reason that in the first place the results of the present ex-

periment give no suggestion that with larger dosage any such result would appear, and in the second place, because the experiments of Bacot and Harden (48) indicate that as slight (or slighter) alterations of the food of *Drosophila* as those of the present experiments may produce marked effects in respect of viability.³

For some reason which we are unable to explain, the flies of Line 107 had, in all the series of this experiment, a lower mean duration of life than this line has ever shown before (*cf.* 32, 44, and section *A* of the present paper). The values are extremely even and consistent in this feeding experiment, but are about 10 days lower than what previous work has indicated as the normal duration of life in this line. There has been no other change in the line, in fertility or other characters. We are inclined to believe that the low values in the present experiments represent merely a temporary secular change (? seasonal) in the duration of life characteristic of the line.

Summary

In experiments involving the determination of the duration of life in 2,990 individual flies, it was found that there was no prolongation of the life of *Drosophila* produced by adding embryonic juice (either from the chick, or from the larvæ of *Drosophila* itself) daily to the food, to the amount of 2 per cent. of the total food material, beginning with the 31st day of the flies' life.

LITERATURE CITED

(The plan of numbering citations is explained in the second of these Studies, AMER. NAT., Vol. 56, p. 174.)

44. Pearl, R. and Parker, S. L. Experimental Studies on the Duration of Life. III. The Effect of Successive Etherizations on the Duration of Life of *Drosophila*. AMER. NAT., Vol. 56, pp. 273-280, 1922.
45. Frisch, A. and Starlinger, W. Zur Frage der Protoplasma-aktivierung. Zeitschr. f. d. ges. exp. Med., Bd. 24, pp. 142-158, 1921.

³ It ought, however, to be pointed out that the experiments of Bacot and Harden are extremely faulty from a technical standpoint. They evidently know little of the practical husbandry of *Drosophila*. Their cultures were incubated at 30° C. At this temperature one does not get anything remotely resembling normal physiological processes or duration of life, except after many months of acclimatization.

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VI. A COMPARISON OF THE LAWS OF MORTALITY IN DROSOPHILA AND IN MAN

PROFESSOR RAYMOND PEARL

I

IN the first of these Studies (27) there were presented for the first time, so far as I am aware, complete life tables for any other organism than man. Up to the present time there have been presented in the published results of the work of this laboratory on *Drosophila* (27, 32, 44, 49, 50) exact determinations of the duration of life in 24,329 individual flies. This is a statistically respectable mass of material, and warrants some general discussion.

In the first study a rough, purely graphical comparison of the l_x lines of the *Drosophila* and certain human life tables was instituted. This comparison, rough as it was, made apparent at once the fact that there was a fundamental similarity in laws of mortality in these two organisms.

It is my purpose in the present paper to make a more exact comparison of the values of the life table functions in the two cases. It will be seen that the similarity is even closer than was supposed from the rough comparison, and that in fact we are dealing here with qualitatively identical expressions of an obviously fundamental biological law.

II

Upon what basis shall any life table function, say l_x , of the *Drosophila* life table be compared with that of man? The life span of one of these organisms is best measured in days, while that of the other is measured in

years. This fact, however, offers no insuperable difficulty to the comparison. What is needed is to superimpose the two curves so that at least two *biologically equivalent* points coincide. The best two points would be the beginning and the end of the life span. But in the case of *Drosophila* our life tables start with the beginning of *imaginal* life only. The larval and pupal durations are omitted. In our preliminary comparison (27) we took human age 15, as the point corresponding biologically to the beginning of imaginal life in *Drosophila*.

I think we can get at this starting point more exactly by putting the human and *Drosophila* l_x curves together as a starting point at the age for each organism *where the instantaneous death rate q_x is a minimum*. In the case of *Drosophila*, I think we are safe in concluding, on the basis of the work of Loeb and Northrop (14-17) as well as from our own observations, that this point is at or very near the beginning of imaginal life. We shall accordingly take *Drosophila* age 1 day as this point. Our life tables show that certainly *after* this time q_x never again has so low a value. Indeed the fundamental law of mortality in *Drosophila* imagoes was stated in (27) in this way (p. 492): "the instantaneous death rate increases with age as a modified logarithmic function of x ."

The latest edition of Glover's (51) United States Life Tables gives (p. 68) for white males in the original registration states the following values for q_x : for age 11-12 2.28, and for age 12-13, 2.29. We may, therefore, with sufficient accuracy take exactly 12 years as the minimum point, particularly as the l_x figures we shall have to use are tabled as of the *beginning* of the age interval.

For the other end of the life span we may conveniently take the age at which there is left but *one* survivor out of 1,000 starting at age 1 day for *Drosophila* and age 12 years for white males. This age for wild type *Droso-*

phila is, to the nearest whole figure, 97 days. To determine it for white males we have Table I, calculated from Glover's Table 9.

TABLE I

SURVIVORSHIP OF WHITE MALES IN ORIGINAL REGISTRATION STATES ON THE BASIS OF 1,000 AT AGE 12

Age	Number Alive at Beginning of Age Interval l_x	Age	Number Alive at Beginning of Age Interval l_x	Age	Number Alive at Beginning of Age Interval l_x
12-13.....	1,000	45-46	803	78-79	194
13-14.....	998	46-47	792	79-80	171
14-15.....	995	47-48	782	80-81	150
15-16.....	993	48-49	771	81-82	130
16-17.....	990	49-50	760	82-83	110
17-18.....	987	50-51	749	83-84	93
18-19.....	983	51-52	737	84-85	77
19-20.....	979	52-53	725	85-86	63
20-21.....	975	53-54	713	86-87	51
21-22.....	970	54-55	699	87-88	41
22-23.....	965	55-56	686	88-89	32
23-24.....	960	56-57	671	89-90	25
24-25.....	955	57-58	655	90-91	19
25-26.....	950	58-59	639	91-92	14
26-27.....	944	59-60	622	92-93	10
27-28.....	939	60-61	604	93-94	7
28-29.....	934	61-62	585	94-95	5
29-30.....	928	62-63	566	95-96	4
30-31.....	922	63-64	546	96-97	2
31-32.....	916	64-65	525	97-98	1.59
32-33.....	910	65-66	504	98-99	1.01
33-34.....	903	66-67	482	99-100	.63
34-35.....	896	67-68	459		
35-36.....	889	68-69	436		
36-37.....	881	69-70	412		
37-38.....	873	70-71	389		
38-39.....	865	71-72	364		
39-40.....	857	72-73	340		
40-41.....	849	73-74	315		
41-42.....	840	74-75	291		
42-43.....	831	75-76	266		
43-44.....	822	76-77	241		
44-45.....	812	77-78	217		

From this it appears that there is almost exactly one survivor at 98 years. So then we have as biologically equivalent life spans

97 days of *Drosophila* life as imago = 86 years
of human life.

Whence it follows that

1 day of *Drosophila* life = .8866 year of human life
and

1 year of human life = 1.1279 days of *Drosophila* life.

III

We are now in position to make an exact comparison between the life tables of the two organisms. This may be done perhaps most instructively by setting up l_x lines for the two forms on the basis of age in *centiles of the life span*, rather than days or years. That is to say, the whole comparable life spans (as defined in this paper) of 97 days in *Drosophila* and of 86 years for white males will each be divided into 100 equal parts, and the survivors at the attainment of the beginning of each centile interval will then be computed.

This is done for wild-type (long-winged) *Drosophila* males (Pearl and Parker (27) Life Table II) and male whites in original Registration states in 1910 (Glover's Table 9), in Table II.

The two life curves of Table II are shown graphically in Fig. 1, plotted on an arithlog grid. We have, in Table II and Fig. 1, for the first time, so far as I am aware, a precise quantitative comparison of the life spans and one of the mathematical functions of the mortality of two different organisms.

It will be noted that:

1. The form of the l_x distributions is fundamentally the same in both of these organisms over the equivalent life spans. Considering the extreme differences in habits of life, structure, physiology, and environmental stresses and strains in the two cases, this is a truly remarkable result. It seems to me to mean that the factors which determine individual longevity, and differences in this character, are biologically deeply rooted, at least as fundamental, apparently, as the factors which determine the specificity in the morphogenesis of organisms, and perhaps even more so. We are accustomed loosely to think that the prime factors in determining

TABLE II

SURVIVORSHIP DISTRIBUTIONS (l_x) FOR EACH CENTILE OF THE COMPARABLE
LIFE SPANS OF (a) WILD TYPE *DROSOPHILA* MALES AND (b)
WHITE MEN IN THE ORIGINAL REGISTRATION
STATES IN 1910

Centile of Comparable Life Span	Numbers Alive at Beginning of Centile Age Interval		Centile of Comparable Life Span	Numbers Alive at Beginning of Centile Age Interval	
	<i>Drosophila</i>	Man		<i>Drosophila</i>	Man
0- 1.....	1,000	1,000	51-52	360	673
1- 2.....	991	998	52-53	344	659
2- 3.....	981	996	53-54	328	645
3- 4.....	972	994	54-55	312	631
4- 5.....	963	991	55-56	296	616
5- 6.....	954	989	56-57	280	601
6- 7.....	945	986	57-58	265	585
7- 8.....	935	983	58-59	250	568
8- 9.....	926	980	59-60	235	551
9-10.....	917	976	60-61	221	533
10-11.....	907	972	61-62	207	515
11-12.....	898	968	62-63	193	496
12-13.....	888	963	63-64	180	477
13-14.....	879	959	64-65	167	458
14-15.....	869	955	65-66	155	438
15-16.....	859	950	66-67	143	418
16-17.....	849	946	67-68	132	397
17-18.....	839	941	68-69	121	377
18-19.....	828	936	69-70	111	356
19-20.....	818	932	70-71	102	335
20-21.....	807	927	71-72	92	314
21-22.....	796	922	72-73	84	292
22-23.....	785	916	73-74	76	271
23-24.....	773	911	74-75	68	250
24-25.....	761	905	75-76	61	229
25-26.....	749	899	76-77	55	208
26-27.....	737	893	77-78	49	189
27-28.....	725	887	78-79	43	169
28-29.....	712	880	79-80	38	151
29-30.....	699	874	80-81	34	133
30-31.....	686	867	81-82	30	117
31-32.....	672	860	82-83	26	101
32-33.....	659	852	83-84	22	87
33-34.....	645	845	84-85	19	74
34-35.....	630	838	85-86	17	62
35-36.....	616	830	86-87	14	52
36-37.....	601	822	87-88	12	43
37-38.....	586	814	88-89	10	35
38-39.....	571	806	89-90	9	28
39-40.....	555	797	90-91	7	22
40-41.....	540	788	91-92	6	17
41-42.....	524	779	92-93	5	13
42-43.....	508	770	93-94	4	10
43-44.....	492	760	94-95	3.43	8
44-45.....	475	750	95-96	2.80	6
45-46.....	459	740	96-97	2.27	4
46-47.....	443	730	97-98	1.84	3
47-48.....	426	720	98-99	1.47	2.11
48-49.....	410	709	99-100	1.18	1.37
49-50.....	393	697	100	.94	.87
50-51.....	377	685			

human longevity are such things as the infectious diseases, exposure to unfavorable environment, etc. But *Drosophila*, which so far as is known has no infectious diseases, and in general meets a set of environmental

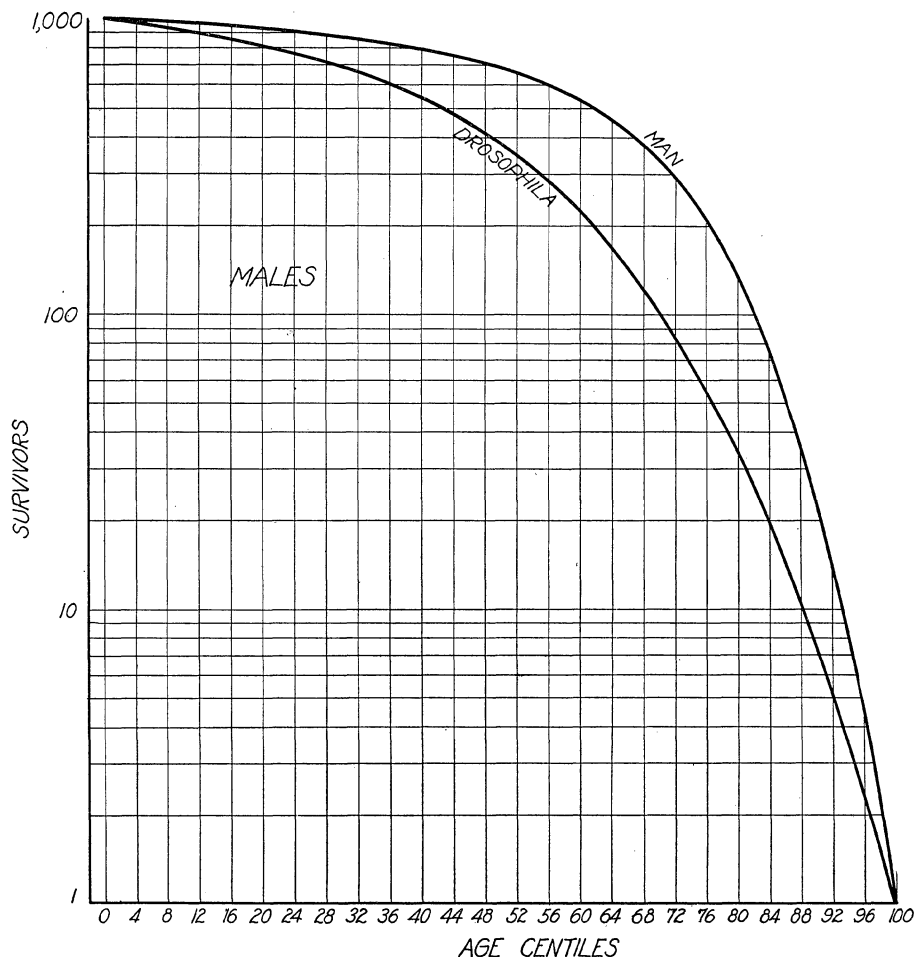


FIG. 1. Comparing the survivorship distributions of *Drosophila* and man (males in both cases) over the equivalent life spans.

conditions wholly different, both qualitatively and quantitatively, from those which operate on man, shows fundamentally the same form of distribution of degrees of longevity.

2. When compared exactly, on the basis of comparable life spans, the human being has at every equivalent age a higher relative expectation of life than does *Drosophila*, measured in terms of its own life span in each case. That this was the case for all but old age was concluded from the rough graphical comparisons of the first Study in this series. It is now seen that the same is true over the whole of life. From this fact the conclusion appears warranted that while the laws of mortality are fundamentally the same *in kind* for *Drosophila* and for man, they differ somewhat quantitatively. There is a temptation to conclude further that the quantitative difference finds its cause in man's own control and amelioration of his environment through sanitation and hygiene. Such a conclusion, however, seems to me not to be strictly warranted, in the light of our present knowledge. There is some suggestion that it is true, as was pointed out in the first of these Studies, from the fact that the progressive change of the human l_x curve in form during historical times has been in the direction of moving from the form typical of *Drosophila* to that now found for progressive, highly civilized groups of men. But definitive conclusions on the point must await further research.

3. The details of the quantitative differences in the two curves are interesting. When the first 25 per cent. of the equivalent life spans has been passed *Drosophila* has lost almost exactly 25 per cent. of the individuals starting life together, while man has lost but 10 per cent. When 50 per cent. of the life spans has been completed *Drosophila* has lost 72 per cent. of the individuals starting together, while man has lost but 31.5 per cent. At 75 per cent. of the life span, *Drosophila* has lost 94 per cent. of the individuals and man 77 per cent. From the 53d centile of the equivalent life spans on practically to the end, man has more than twice as many survivors out of a thousand starting together as does *Drosophila*.

Exactly similar results to those here presented are ob-

tained if one compares human and *Drosophila* life curves for females. Since nothing new in principle is brought out, it is not thought necessary to present the female curves here.

IV

In this paper it is shown that if we take as equivalent life spans in *Drosophila* and man the period between (*a*) the point in the life history of each organism where the specific death-rate (q_x) is a minimum, and (*b*) the point where there is one survivor out of 1,000 starting at the beginning as defined in (*a*), and then divide these equivalent life spans into 100 portions (thus measuring age not in absolute units but in centiles of the life span), the laws of mortality are fundamentally the same in kind in the two organisms. There is a quantitative difference expressible in the statement that at each centile age throughout the life span the number of survivors, out of the same original number starting together, is higher in man than in *Drosophila*.

In a subsequent paper, I hope to take up in detail the functional relations (in a mathematical sense) between the human and *Drosophila* equivalent l_x curves here presented.

LITERATURE CITED

(The plan of numbering citations is explained in the second of these Studies, AMER. NAT., Vol. 56, p. 174.)

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